Dinoflagellate cyst population evolution throughout past interglacials: Key features along the Iberian margin and insights from the new IODP Site U1385 (Exp 339)

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ABSTRACT

IODP 339 Site U1385 ("Shackleton site", e.g. Hodell et al., 2013a), from the SW Iberian margin, offers the opportunity to study marine microfossil population dynamics by comparing several past interglacials and to test natural shifts of species that occurred across these warm periods, in a subtropical context. Here, more specifically, we present results obtained for the dinoflagellate cyst (dinocyst) population integrated at a regional scale thanks to the addition of data from proximal sites from southern Iberian margin. When possible, observations made using the dinocyst bio-indicator are compared to additional proxies from the same records in order to test the synchronicity of the marine biota response. Pollen data available for some of the compiled marine sequences also offer the opportunity to directly compare marine biota with terrestrial ecosystem responses. This spatio-temporal compilation reveals that, over the last 800 ka, surface waters around Iberia were tightly coupled to (rapid) climate changes and were characterised by coherent dinocyst assemblage patterns, highlighting a permanent connection between Atlantic and Mediterranean waters as evidenced through a continuous exchange of dinocyst populations. Some index species well illustrate the evolution of the regional hydrographic context along time, as for instance *Spiniferites* and *Impagidinium* species, together with *Lingulodinium machaerophorum, Bitectatodinium tepikiense* and heterotrophic brown cysts. They constitute key bio-indicators in context of natural environmental shifts at long and short timescales.

KEYWORDS: dinocysts, interglacials, biodiversity and climate shifts, southern Iberian margin

1. Introduction

Drastic marine biodiversity changes that occurred over the last century raise key questions today in connection with the concept of ecosystem resilience to environmental changes (e.g. Millenium Ecosystem Assessment synthesis reports, 2005). This is especially true for neritic ecosystems that encountered major perturbations especially related to the geochemical balances of sea-surface waters (e.g. eutrophication, pollution contaminants, acidification e.g. Crutzen, 2002) but also to physical parameters (e.g. SST warming, sea-level changes, river nutrient loads). At present, natural environmental trends are hidden by anthropogenic forcings and reference points are lacking. The natural state is only found in the recent past, outside of the modern instrumental period (i.e. the last century), thus preventing actualistic studies from defining robust baselines for environmental predictions and trajectories. Paleostudies carried out on fossil sediment archives thus provide invaluable information (e.g. Wilis et al., 2010) even if they are integrating only a partial view of the paleo-biodiversity, being only indirectly and incompletely representative of past biomes and biotopes. Interglacial optima, and especially their surrounding transitional periods (both deglaciations and glacial inceptions), represent key intervals where ecosystems, comparable to modern ones, could be tested along large amplitude ecological shifts (e.g Willis et al., 2010). They permit us to test if the marine biota offers the same recurrent kind of transient populations during such shifts and if so, to picture characteristic patterns that could be recognized within the assemblages. Are there typical species that could be considered as

pioneers, opportunistic or pre-adapted, and so repetitive scenarios that could provide us with a predictive ecological model for the marine biota evolution?

For this study we based our approach on the dinoflagellate cyst (dinocyst) proxy, an organic-walled bio-indicator related to the phytoplankton realm which constitutes sexual reproduction remains of some dinoflagellate species (e.g. de Vernal and Marret, 2007; Ellegaard et al., 2013). Fossil dinocysts have long been used in Mesozoic-Cenozoic paleoceanographic studies to reconstruct past hydrographical patterns qualitatively as well as quantitatively through transfer functions (e.g. Wiliams, 1971; Turon, 1978; de Vernal et al., 2001; Houben et al., 2012; de Schepper et al., 2013; Mertens et al., 2014). They constitute a robust planktic group to document past sea-surface ecological changes (e.g. Marret and Zonneveld, 2003; Zonneveld et al., 2013) and are especially powerful in neritic environments where their motile thecal forms proliferate preferentially (e.g. Dale, 1983; Dodge and Harland, 1991).

Here we compare the evolution of dinocyst relative abundances across four of the most studied interglacials with regard to their climate dynamics: Marine Isotopic Stage (MIS) 1, 5, 11 and 19. We thus gathered sedimentary sequences (along which dinocyst assemblages have been analysed at high resolution) from the south-western European margin (Iberia), from its Atlantic side as well as from the inner Alboran Sea. This compilation, providing an integrated view of dinocyst assemblage evolution in space and time from a sensitive subtropical area (e.g. Giorgi, 2006), includes new original analyses on the IODP 339 Site U1385 (Hodell et al., 2013a and b). It gives us the opportunity to: i) document poorly known dinocyst populations from the interglacial MIS 19 and 11, and ii) study ecological interactions through several climate cycles of the Quaternary between two end-member environments

on either sides of the Gibraltar strait: the Mediterranean Basin (residual Tethys) and the North Atlantic.

2. Environmental setting: key features

The modern hydrography of the southern Iberian margin is mainly forced by water mass exchanges with North-Atlantic waters penetrating the Alboran Sea at the surface, whereas deep saltier waters exit the Mediterranean at depth (Mediterranean Overflow Water or MOW). This scheme is mainly related to contrasted density budgets in between the two respective basins, however modulated by atmospheric forcing throughout the transfer of wind stress to surface currents, such as the Azores and Portugal currents for the Atlantic, or the western/ eastern anticyclonic gyres associated with the Algerian current for the Alboran (e.g. Rohling et al., 1995; Johnson, 1997; Font et al., 2000; Mauritzen et al., 2001; Arístegui et al., 2005, 2009, see Figure 1). This dynamical pattern evolves seasonally /yearly according to meridional shifts / contractions - extensions of the subtropical North Atlantic gyre, inducing changes in the temporality of upwelling cells and thus major modifications of the sea-surface productivity conditions (Arístegui et al., 2005; Peliz et al., 2005; Relvas et al., 2007). At millennial time scales, significant modulations of the MOW have been recorded during major climate transitions associated with boreal ice-sheet collapses (i.e. the well-known Heinrich events, e.g. Heinrich, 1988) with a consensus supporting synchronous accelerations of MOW during these cold episodes (e.g. Cacho et al., 2000; Voelker et al., 2006; Rogerson et al., 2010). This also resulted in drastic consequences in water mass

surface exchanges with the reorganisation of the Alboran gyres and obvious impacts on sea-surface productivity on either sides of Gibraltar (Penaud et al., 2011).

3. Methods

This study relies on new unpublished data (IODP 339 Site U1385 MIS 19 and 11 sections - i.e. from the 788-749 ka and 410-384 ka age intervals respectively - from the "Shackleton site", e.g. Hodell et al., 2013a,) and also gathers several previously published and unpublished dinocyst records from the Southern Iberian margin (Figure1; see Table 1 for key elements concerning each studied core). We selected marine sequences that could provide us a fine enough analytical resolution regarding dinocyst assemblage patterns through time and where comparative data exists from other paleoenvironmental proxies (mainly derived from planktic foraminiferal and pollen assemblages, mono-specific foraminifera $\delta^{18}O$).

Site U1385 was drilled from the SW Iberian Margin during IODP Expedition 339 (e.g. Hodell et al., 2013a) with the aim of extending further back in time the range of the exceptional piston cores previously retrieved in this area (including those listed in Table 1). Its stratigraphy was built upon a combination of chemo-stratigraphic proxies (Hodell et al., 2013a; this volume), i.e. Ca/Ti ratio, measured in all holes by XRF core scanning to construct a composite section, coupled to benthic foraminifera oxygen isotopes which were correlated to the marine $\delta^{18}O$ LR04 stack (Lisiecki and Raymo, 2005). More details regarding this stratigraphical work can be found in Hodell et al. (2013a and b; this volume). Concerning the

other published paleoceanographical records used in this study, we strictly used the age models as initially established and published by the authors (cf. Table 1).

Palynological preparations were conducted on IODP 339 Site U1385, Hole D, Core 10H between sections 3 and 6 which encompass MIS 19 and on Hole D, Core 7H section 1 and Hole E, Core 6H sections 5 and 6 for MIS 11. The preparation techniques follow standard procedures and can be found at http://www.epoc.u-bordeaux.fr/index.php?lang=fr&page=eq_paleo_pollens. Acetolysis was not employed to avoid destruction of heterotrophic dinocyst taxa such as Polykrikaceae and *Brigantedinium* cysts (Marret, 1993; Combourieu-Nebout et al., 1998; Kodrans-Nsiah et al., 2008). The samples were used together for dinocyst and pollen analyses (Sànchez-Goñi et al., this volume) with two set of slides mounted independently to facilitate each kind of observations (i.e. glycerine jelly coloured with fushine for dinocysts and bidistilled glycerine for pollen). Dinocysts were counted on the fraction 10-150 µm (from 47 to 365 -average 187- specimens per sample) using a Zeiss PrimoStar light microscope at x400 magnifications. Identifications were based on Turon (1984), de Vernal et al. (1992) and Rochon et al. (1999). The nomenclature conforms to Fensome et al. (1998) and Fensome and Williams (2004), and dinocyst assemblages were described by the percentages of each species calculated on the basis of the total dinocyst sum including unidentified taxa and excluding pre-Quaternary specimens. Palynomorph absolute concentrations (number of dinocysts/cm^3) were calculated using the marker grain method (Stockmarr, 1971; de Vernal et al., 1999; Mertens et al., 2009).

A composite sequence was built (for what we have called the "SHACK area", i.e. green circle on Figure 1) using relative abundances of dinocysts from the twin cores SU81-18 (MIS 1 to

2), MD95-2042 (MIS 2 to 6) and IODP 339 Site U1385 (MIS 11 and 19, "Shackleton site" sensu Hoddel et al., 2013a). A Principal component analysis (PCA) was applied to this raw data set (non- transformed relative abundances) using the XLSTAT software (XLSTAT Version 2015.4.01.19992 @Addinsoft 1995-2015, http://www.xlstat.com/en/). The training dataset and the PCA results can be downloaded on line as *Supplementary information* (SI). Additionally, some coherency tests were done using the XLSTAT and PAST (Hammer et al., 2001) softwares for the comparison of thermophilous indexes derived from pollen (Mediterranean forest) and from dinocysts. Two indexes were used for dinocysts: (a) the warm *Impagidinium* sum: $\Sigma W_{Impagidinium}$, cumulating relative abundances of the tropical/subtropical *I. patulum* and *I. aculeatum* species and of the subtropical/temperate *I. paradoxum* and *I. sphaericum* species; (b) the warm/ cold dinocyst ratio as defined in Combourieu-Nebout et al. (1999), i.e. [W/(W+C)] , where (W) cumulates warm-water indicator species: i.e. *Spiniferites mirabilis* s.l. (= *S. mirabilis + S. hyperacanthus*), *Selenopemphix nephroides*, *Impagidinium patulum, Impagidinium strialatum, Operculodinium israelianum, Spiniferites delicatus*, and *Spiniferites membranaceus*, excluding *Operculodinium centrocarpum* considered to be too ubiquitous, whereas (C) gathers cold-water indicators, namely: *Nematosphaeropsis labyrinthus, Bitectatodinium tepikiense, Spiniferites elongatus, Impagidinium pallidum, Pentapharsodinium dalei* and *Islandinium minutum.*

4. Trends and common features in dinocyst communities during climatic optima and their transitions

For the following discussion, we consider the main features detected in the assemblages over time. Our interpretations are based on dominant dinocyst species and also, in some cases, on biostratigraphically significant ones. A detailed picture of selected significant dinocyst species is provided for the SHACK area (MD95-2042/SU81-18 and IODP 339; Figure 2) since MIS 11 (from 410-384 ka) and MIS 19 (788-749 ka) analyses constitute new dinocyst results for this area.

The compilation made for the Southern Iberian margin is mainly based on the comparison of three specific/index groups, that dominate alternatively dinocyst assemblages and showed a sensitive response to climate shifts through time (Figure 3): i) heterotrophic taxa (sum established after the taxa list of Marret and Zonneveld, 2003), ii) warm *Impagidinium* species (sum of subtropical *I. patulum* and *I. aculeatum* species, also grouped with temperate *I. paradoxum* and *I. sphaericum* species), and iii) the species *L. machaeorophorum*.

In the SHACK area, autotrophic taxa are marked by the dominance of well-known temperate to cosmopolite species: *Lingulodinium machaeorophorum*, *Nematosphaeropsis labyrinthus*, *Operculodinium centrocarpum sensu* Wall and Dale (1966), cysts of *Pentapharsodinium dalei* together with numerous species from the *Spiniferites* group, including *S. mirabilis* s. l. and *S ramosus* s. s. (Figure 2). Heterotrophic dinocysts are mainly represented by *Brigantedinium* species (*B. cariacoense* and *B. simplex* included) together with *Peridinioid* taxa such as *Selenopemphix quanta* or *Selenopemphix nephroides* (Plate 1). In this group, it is worth noting the common occurrence of cysts of *Protoperidinium stellatum*, which will herein be refer to the usual binomial name "*Stelladinium stellatum*" (Plate 1) for practical reasons and in order to be consistent with reference recent works (e.g. Zonneveld et al., 2013) and with the Sprangers et al. (2004) dinocyst inventory study from modern sediments of the Iberian

margin. In the MIS 19 section of IODP339 1385, *S. stellatum* abundances reach up to 7% of the total dinocyst assemblage (Figure 2), while this taxa was not observed in any of the most recent interglacials MIS 11, 5 and 1 from the twin cores MD95-2042 and SU81-18 (Eynaud, 1999; Turon et al., 2003). A similar assemblage pattern was also observed for the Alboran site ODP976 over a longer time scale (see Fig.2 in Combourieu-Nebout et al., 1999), with also an almost disappearance of *S. stellatum* for time periods following the Mid-Brunhes Event (MBE). On the basis of our compilation, the highest occurrences of *S. stellatum* observed during MIS 19 (between roughly 750 and 800 ka BP) could thus sign a specific biostratigraphic event. At present, this species is characteristic of hypertrophic environments and was used as a marker of eutrophication in historical times (e.g. Shin et al., 2010 in the East China and Japan seas; Zonneveld et al., 2012 in the Adriatic and Ionan seas). Furthermore, on the basis of sediment trap analyses from the Mauritanian upwelling zone, Zonneveld et al. (2010) related the ecology of *S. stellatum* and its seasonal dynamics to those of *L. machaeorophorum*. It has also been described from modern sediments of the Gulf of Mexico (Limoges et al., 2013), in Brittany Bays (Larrazabal et al., 1990), and identified as a potential proxy of sea-level rise over the last glacial-interglacial period by marked increases of this species detected at 16 ka BP in near-equatorial latitudes of the Western African margin (Hardy et al., in prep).

Among the *Spiniferites* species, *S. ramosus* and the rare taxa *S. rubinus* (e.g. Harland, 1992; Head et al., 1996) also display noticeable biostratigraphic trends in relation to MIS 19: Between 750 and 800 ka, *S. ramosus* shows percentages two times higher than modern values recorded in the area (e.g. Rochon et al., 1999), and then shows a progressive decline until present (Figure 2 and 4). *S. rubinus* appears as specifically related to the beginning of MIS 19. Their cumulative abundances reached up to 30% of the assemblage at 784 ka.

4.1. L. machaeorophorum and heterotrophic dinocysts: when past data put to test modern ecology knowledge

Figure 3a provides an integrated peri-Iberian picture of dinocyst specific changes that occurred during interglacials and subsequent glacials in order to identify coherent ecological adaptations of this group through time. Climate changes are illustrated in parallel through planktonic $\delta^{18}O$ signals obtained on the same cores (when available), the global LR04 benthic stack (Lisiecki and Raymo, 2005), and summer insolation values at 65°N (Berger and Loutre, 1991).

Especially obvious in all studied records is the opposition observed between the occurrence of heterotrophic dinocysts and *L. machaeorophorum*, which seem to exclude each other. Except during MIS 1, these two species show opposite patterns with the expansion of heterotrophic species during cold periods (percentages ≥ 80% reached during the last glacial) and of *L. machaeorophorum* during transitional periods (comparable high near monospecific values only recorded during glacial inceptions). This is especially evident for MIS 19, 11 and 5 but should be shaded for MIS 1 where the *L. machaerophorum* high abundances occur early just after the Termination I. The species *L. machaerophorum* (related to the motile dinoflagellate *Lingulodinium polyedrum*) is a widely distributed dinocyst (e.g. Rochon et al., 1999) but is especially concentrated today in coastal/neritic sediments around the Gibraltar strait (Williams, 1971; Marret and Zonneveld, 2003; Zonneveld et al., 2013; Penaud et al., in prep). This local high occurrence is particularly interesting as this species could then be used as a peculiar taxa index for the present study. *L. machaerophorum* also colonizes estuarine

environments (Morzadec-Kerfourn, 1977, 1992) and is frequently associated with eutrophic areas (fjords especially, e.g. Sætre et al., 1997, Dale et al., 1999, but not restrictively e.g. Zonneveld et al., 2012). As such, Leroy et al. (2013) recently considered its highest occurrences in the Caspian Sea as a biostratigraphical marker for the Anthropocene. Finally, it was interpreted as a proxy for past huge river discharges into the Ocean (Zaragosi et al., 2001; Eynaud et al., 2007; Penaud et al., in prep) and even considered as allochtonous in marine waters by Turon and Londeix (1988). Blooms of its motile form can be responsible for toxic red tides (Moorthi et al., 2006) and some culture experiments demonstrated that this species is highly sensitive to the water column stratification (Thomas and Gibson, 1990; 1992).

At present, *L. machaerophorum* distribution in modern sediments matches fairly well with the distribution of heterotrophic species, with high abundances preferentially found in coastal regions and close to upwelling cells (e.g. Zonneveld et al., 2013). It questions the observed patterns in our records where these species rather seem to oppose: (1) are they related to nuanced ecological patterns such as seasonality, i.e. shifts from permanent to seasonal upwelling regimes (or vice-versa) which could have induced major changes in dinocyst communities, or (2) are they due to preservation and/or cyst transportation changes along time? Preservation is especially a critical issue as dinocyst species are not equally impacted by oxydation in the water-column and after deposition (e.g. Zonneveld et al., 1997, 2012; Zonneveld and Brummer, 2000; Bogus et al., 2012): some of them being very sensitive to water oxygen concentrations and thus water sources and dynamics. It is generally accepted that brown cysts, mainly produced by heterotrophic dinoflagellates (i.e. *Protoperidinium*) are more sensitive to aerobic degradation than *Gonyaulacoid* derived cysts (e.g. Dale, 1976). Among our index taxa for this comparative study, *L. machaerophorum* and

warm *Impagidinium* species are respectively classified as moderately sensitive and resistant to oxygen availability in bottom waters (de Vernal and Marret, 2007).

Does the observed pattern thus signify a difference in bottom water-mass properties (and thus circulation) rather than a sea-surface productivity change, or is it a combination of both processes? In our study, the inter-basin comparison can provide some clues to solve this question, as the opposition between heterotroph cysts and *L. machaerophorum* are systematically observed whatever the considered period and basin. Such a coherent pattern suggests a similar way of cyst production and/or preservation despite distinct local surface and bottom conditions. It is highly improbable that interglacial/ glacial changes cancelled these hydrographical differences since dinocyst population changes are not perfectly synchronized between the two basins, thus also underlining their own specificities through time. Therefore, the alternative solution would be to consider that the observed downcore antiphase between heterotroph cysts and *L. machaerophorum* is not a matter of post-production/preservation biases. Then, how to reconcile quite similar modern biogeographies which, in past times, seemed to exclude each other? Modern *L. machaerophorum* ecological requirements are still far from being correctly identified and this species may represent simply an opportunistic species. Interestingly, *L. machaerophorum* dynamics observed from our compilation (Figure 3) reveals that this species follows or precedes maximal expansion of warm sea-surface taxa during interglacial optima. This shift is then discussed below.

4.2. Warm *Impagidinium species* along interglacials: what do they reveal?

In this study, the probable most significant dinocyst assemblage we retained is the one associated with *Impagidinium*. These typical oceanic taxa, often thermophilous, are among the common dinocysts found in the area (e.g., Turon et al., 2003; Penaud et al., 2011). For this work, we have lumped together abundances of warm Impagidinium ($\Sigma W_{Impagidinium}$) to define a specific index of warm sea-surface conditions ,for which we have tested coherency through time and from one basin to another (Figure 3 and 4, see also SI for further details regarding this group). At present, maximum abundances of these species are recorded in sediments of the equatorial Atlantic Ocean with a preference for full marine waters (Zonneveld et al., 2013). In the studied records, highest $\Sigma W_{Impagidinium}$ values (i.e. >10%) are associated with the onset of warm conditions during climatic optima (as defined from low isotopic values plateau, Figure 3a). Their expansion is noticeable during short periods only, of maximum duration of 10 ka, in close phasing with negative shifts in the planktonic $\delta^{18}O$ signal. They seem specifically to mark post-glacial warm conditions rather than hypsithermal periods (Figure 3). The relative short duration of expansion of these warm *Impagidinium* is easily explained by competition stress with other thermophilous taxa such as *S. mirabilis* (see Turon and Londeix, 1988; Eynaud et al. 2000, Penaud et al., 2008, 2011 for discussions). It could also typify a peculiar ecological strategy as a pioneer group and/or as accompanying a change in the oceanic circulation as it was already suggested by Londeix et al. (2007).

For MIS 5, $\Sigma W_{Impagidinium}$ increases parallel the three isotopic sub-stage lightening and coincide well with insolation maxima (pink bands on Figure 3a). When comparing the intrinsic dynamics of each interglacial optima in the SHACK area (Figure 3b) by synchronizing Terminations (here Terminations I, II and IX after Lisiecki and Raymo, 2005), and despite differences in temporal resolution analysis, trends in the $\Sigma W_{Impagidinium}$ show similar pacing

along interglacials. This is especially obvious for peaks observed just after Terminations and for the glacial inception following interglacial optima.

Furthermore, the multi-phased interglacial complexes MIS 19 and MIS 5 are also well reflected in the $\Sigma W_{Impagidinium}$ evolution. Amplitudes for MIS 1 (green curve; Figure 3b) are noticeably largest than those of previous warm MIS (blue and red curves; Figure 3b), probably resulting from a major dinocyst community change through time, implying a growing presence of *Impagidinium* species associated with a synchronous general decline of *Spiniferites* species (as previously pointed out).

Figure 4 synthesizes the most salient features provided by dinocysts and pollen (here the Mediterranean forest) for a composite sequence consisting of cores SU81-18 (e.g. Turon et al., 2003), MD95-2042 (e.g. Eynaud et al. 2000; Shackleton et al., 2003) and IODP 339 1385 (this work, Sànchez-Goni et al., this volume). Additionally we plotted alkenone-derived SST from core MD95-2042 (MIS 1 and 5 sections after Pailler and Bard, 2002) and from the proximal core MD01-2443 (MIS 11 section after Martrat et al., 2007). Percentages of the polar taxa *Neogloboquadrina pachyderma* sinistral (*Nps*) are also shown (from core SU81-18 MIS 1 after Turon et al., 2003, for core MD95-2042 MIS 5 after Sànchez-Goñi et al., 2006; for core MD01-2443 MIS 11 after Voelker and de Abreu, 2011). This data set is also compared to the Marine $\delta^{18}O$ stack LR04 (Lisiecki and Raymo, 2005) and to summer insolation at 65°N (Berger and Loutre, 1991). Periods of maximum values of $\Sigma W_{Impagidinium}$ are marked by pink bands. They provide evidence of discrete warming episodes that took place near Terminations I, II and IX, that we can also directly compare with synchronous proximal continental responses regarding Mediterranean forest evolution. From this compilation, sea-

surface warming events appear synchronous with warming detected on land at millennial scales. A test of correlation was done to check this synchronicity giving a r^2 of 0.270 (results obtained with the Past software, see SI). The reader should keep in mind that pollen and dinocyst preparations are observed from same slides, coming from identical laboratory procedures, thus implying no artefact when correlating palynological ocean-continent data. Such a result confirms previous observations made for MIS 5 and 3 on the same site (Sànchez-Goñi et al., 1999, 2000; Eynaud et al., 2000) and permits us here to confirm and extend the continental / ocean relationship up to 800 ka.

In contrast to $\Sigma W_{Impagidinium}$, high abundances of *Bitectatodinium tepikiense* are observed during cold phases, also characterized by high *Nps* percentages. A strong representation of *B. tepikiense* is especially noticeable during cold MIS 5 interglacial substages. Cold phases are also marked by high absolute abundances of dinocysts (i.e. concentrations in nb of cysts /dry cm^3) in sediments. These high concentrations were already noted by several authors on this margin during cold climatic events (e.g. Zippi, 1992; Eynaud, 1999; Eynaud et al., 2009; Penaud et al., 2010; 2011) and interpreted as representing changes in the local upwelling dynamics (from seasonal to year-round) in response to atmospheric re-organisations. This interpretation was based on the distribution of modern dinocyst concentrations in the sediments from the proximal North Canary Basin, which show high dinocyst concentrations within zones marking upwelling filaments (e.g. Targarona et al., 1999; Bouimetarhan et al., 2009b). Conversely, on the SW Iberian Margin (Figure 1), Zippi (1992) noted an opposite relation between carbonate content and dinocyst concentrations in the sediment and attributed that observation to the preferential dissolution of carbonate under cold climate (and thus the artificial increase of cysts) in concordance to a high index of fragmentations of planktonic foraminifera shells. However, Zippi (1992) did not introduce any consideration

about the paleoproductivity issue. Indeed, for calcareous (foraminifera) as well as for organic-walled (dinocysts) material, the residual concentration of microfossils in sediments is the result of a complex balance between production, dissolution and preservation. Thanks to the close correlation made in this study between marine and pollen data, we directly attribute the modulation of dinocyst concentrations to climate.

5. The significance of population shifts: from ecology to oceanic circulation patterns

The dinocyst compilation made in this study provides important biodiversity information that could be tied to changes in the local and/or regional hydrographical dynamics in response to climate changes. Population shifts occur repetitively and coherently through time with some index groups that could be used to evaluate the adaptation capability of the marine flora. They illustrate a constant population interchange between the western Mediterranean and the subtropical North Atlantic despite sea-level changes and the temporal physiographic barrier of the Strait of Gilbraltar, which should have reduced water exchanges during low sea-levels of the last million years. These latter processes have had important echoes on planktonic populations, as demonstrated by Rohling et al (1995) for planktonic foraminifera, something also detected with some dinocyst key taxa.

Strong modulations of the MOW have already been pointed out by several studies for the last glacial (e.g. Cacho et al., 2000; Voelker et al., 2006; Rogerson et al., 2010), showing an acceleration of the outflow during cold phases. Their impact on the distribution of dinoflagellate and their cysts has certainly been important. A southward migration of

biogeographical provinces in the North Atlantic and even the invasion of the Alboran Sea waters by *B. tepikiense* from where this species is absent at present (Turon and Londeix, 1988; Combourieu-Nebout et al., 2002; Penaud et al., 2011; Figure 3) have been observed concomitantly. This invasion, in a configuration of accelerated MOW, attests to an extensive North Atlantic intrusion in the Alboran Sea, probably as a way to compensate the MOW export and its associated deficit. This thus supposes vigorous Atlantic/Mediterranean exchanges at those times and thus enhanced exportation/importation of cysts.

Cold sub-stages within interglacial complexes (MIS 19 and 5) demonstrate the same biotic pattern with also high occurrences of *B. tepikiense* (this work, Combourieu Nebout et al., 1999; Eynaud et al., 2000). The context is however different here even if some analoguous hydrographical mechanisms could be at play, i.e. due to acceleration of the MOW also, but in this case rather forced by a reduction of the Gibraltar strait section during cold sub-stages and associated sea-level low stands (the reader should keep in mind that at the opposite HEs record a rising sea-level with an estimated magnitude of up to 30 m, e.g Siddal et al., 2003). The synchronous regression of warm species and of *L. machaerophorum* furthermore documents a severe cooling and a major change of the water column stability; a vital requirement for this later species as deduced from culture (e.g. Thomas and Gibson, 1990). Turbulence at the Gibraltar strait due to the acceleration of currents, thus preventing a soft settling of cysts and inhibiting a complete life cycle, could explain the *L. machaerophorum* disappearance. This turbulence could be amplified by atmospheric processes, i.e. winds, the regression of the Mediterranean forest on Iberia being also noticed (Figure 3).

The past population shifts observed in this part of the sub-tropical North-Atlantic provide some new insights regarding the known modern ecology and biogeography of cysts and their

related theca (i.e. Marret and Zonneveld, 2003, de Vernal and Marret, 2007). They show a strong potential for dinoflagellates to adapt, even when facing abrupt ecological changes. Two taxa would especially be considered as super-adapted to transient periods: one is a common typical cyst from the studied area, *L. machaerophorum;* the other, *B. tepikiense,* is a taxa rather distributed in the cool temperate Atlantic but especially adapted to strong seasonality (i.e. cold winters and warm summers), as those which characterize waters from the St Laurent outlet at present (e.g. Rochon et al., 1999). These two species are found at the transition boundaries of interglacial optima and could thus be qualified of opportunistic, as conditions accompanying transition phases (glacial inception and termination) are especially unstable and contrast with the relative equilibrium of warm optima. However the local high occurrence of *L. machaerophorum* rather argues for a pre-adaptation to the sea-surface conditions surrounding the Gibraltar strait. Conversely, its presence with nearly mono-specific abundances in the modern sediments from the Iberian and North Canary regions since 5 ka at least (Figure 2) questions the hydrographic and associated climatic modes of the last millennia. When comparing its specific dynamics during previous interglacials, this species does not mark hypsithermal modes but rather cooler conditions. This supports previous findings showing that modern conditions around Iberia already shifted toward a late Holocene Neoglacial state (e.g. Jerardino, 1995). For the Atlantic side, it seems to have already implied changes in the seasonality of the modern Canary Current upwelling (e.g. Abrantes et al., 2011; Mc Gregor et al., 2007; Bouimetarhan et al., 2009a).

6. The nine past and current interglacials: new insights from dinocyst data of the "Shackleton" site

Even if not continuous, the dinocyst data produced for this compilation gathering cores from the SHACK area (Figure 1) offer the possibility to test the significance of this phyto-planktonic population regarding long term records over the last 800 ka. The purpose of our approach was to test interglacial periods in low eccentricity contexts first, explaining why, up to date, our focus and records are thus restricted to some snapshots. To present a comprehensive view of these results and simplify the message brought by dinocyst assemblages, we ran a PCA on the composite "SHACK" sequence (SU81-18 /MD95-2042 /IODP339 U1385, see methods and SI). The coordinates of the first three axis obtained from this PCA are plotted along time on Figure 5 and compared to selected 800 ka-long-sequences of interest, along with the [W(/(C+W)] dinocyst ratio for the SHACK area and for the Alboran ODP976 record which, even if of lowest resolution, encompasses the last 810 ka (Combourieu-Nebout et al., 1999). A schematic index reflecting qualitatively the Aguhlas linkage dynamics (as redrawn from Caley et al. 2012) is also plotted to further document inter-oceanic exchanges.

This comparison reveals very distinctive patterns and specific signatures (Figure 5 and SI) for each of the first three PCA-axis (these 3 axis representing nearly 30% of the total variance, see methods and the excel file provided in SI for detailed results of the PCA). These signatures could be summarized as follow: (a) a first axis F1 (13.6 % of the total variance), positively related to warm eutrophic species but negatively related to cold eutrophic ones (see species/ variables distribution in SI), thus bearing the double and coupled environmental signal of SST and upwelling dynamics. Considering a paleoceanographic

perspective, this axis clearly relates to global changes as seen throughout the (ice-volume/ sea-level linked) LR04 record and the CO_2 atmospheric content.

(b) a second axis F2 (7.65 % of the total variance), also bearing a strong SST/ upwelling signature but for which species positively correlated to, are representative of the typical Iberian margin modern dinocyst assemblage (i.e. Sprangers et al, 2004). Its time distribution shows a close matching with the Ca content (vs terrigeneous components) of marine sediments from the subtropical North Atlantic western margin as derived from XRF data, both for the same "Shackleton site" (Log (Ti/ Ca) from Hoddel et al., 2013a and b) and from the southern core MD03-2705 (Malaizé et al., 2012).

(c) a third axis F3 (7.33% of the total variance), which plainly separates autotrophic from heterotrophic dinocyst species, and is interestingly closely mirroring the monsoon index along time (after the stack produced by Clemens et al., 2008).

From this 810 ka long perspective, arise some noticeable points which shed light on the high sensitivity of dinocyst communities regarding climate changes. First of all, it is worth noting the good reproducibility of the [W(/(C+W)] ratio at the regional scale except during MIS 19 where the "Shackleton site" reveals much more contrasted responses. Differences in time resolution are at the origin of this discrepancy but other evidences are brought by the PCA that this MIS 19 interval is clearly atypical. This is well expressed in the F1 component which registers large and sharp amplitude shifts (not seen later in the Pleistocene neither in the Holocene) and additionally shows poor matching with other 810 ka records as plotted on Figure 5. Conversely, F2 and F3 during MIS 19 closely mirror the Ca sedimentary content and the monsoon index respectively, recording synchronous and consistent transitions, thus suggesting that the message brought by dinocyst populations from the Iberian margin is however comprehensive enough to be assimilated to large scale environmental changes

over the last 810 ka. The link between the Ca content and PCA axis 2 is easily understandable at the scale of the North Atlantic basin (including its marginal seas) as it reflects mainly biogenic carbonate content and thus the pelagic production, well known to be favoured, during warm periods (e.g. Chapman and Shackleton, 1997; Richter et al., 2007; Hodell et al., 2013b). In the same way, consistency between the stacked monsoon index vs the PCA axis 3 could be explained by the fact that this axis is mainly representing the weight of autotrophic species which thereby need sea-surface fertilisation and thus dust arrival to proliferate. Most problematic is the signal detected with the PCA axis 1 during MIS 19, which if it does echo the [W(/(C+W)] ratio and the Ca content within the "Shackleton site", is not completely attributable to long term and global trends as stated previously. Is this difference related to the specific assemblage we encountered during MIS 19, with the occurrence of atypical species such as *S. stellatum* and *S. rubinus*, and the high percentages of *S. ramosus* as previously underlined? Could the drastic climatic transitions occurring between MIS 19 and modern times, i.e. the MPT and the MBE, have impacted dinocyst population of this area so significantly? This is highly possible, as these two climatic temporal nodes are known to sign major oceanic reorganisations, with especially a strong impact on the Atlantic meridional oceanic circulation (e.g. Poirier and Billups, 2014; Bell et al.,2015), a key component for the Iberian margin oceanography and its associated upwelling dynamics. To valid such an assumption we urgently need to further extend our record up and back in time, putting a focus not only on past interglacials but also on glacials, including the atypical MIS 13 and MIS 6 ones, so as to detect an optimal set of contrasted features.

7. Conclusions

This study was designed to provide new biogeographical and stratigraphical patterns for the Iberian margin by compiling micropaleontological records derived from the study of dinoflagellate cysts during past interglacials. This effort has revealed that surface waters around Iberia were characterised over the last million years by the repetitive occurrence of the same dinocyst assemblage; however, some discrepancies in the response of this marine protist community shade its adaption to glacial and interglacial cycles. Very coherent features occur on both sides of the Gibraltar strait indicating a constant interchange of populations and a permanent connection between Atlantic and Mediterranean marine biomes, even during sea-level low stands. Regarding dinocysts, this interchange is easily attributed to sea-surface water exchanges, but the Mediterranean Outflow Waters could also be considered as a vector of settled cysts. Some index groups could be used to evaluate the adaptation capability and the dynamics of the marine dinoflagellate flora, especially the autotrophic cysts: *Lingulodinium machaerophorum*, *Bitectatodinium tepikiense*, together with some species from the *Spiniferites* and the *Impagidinium* groups, which swing with heterotrophic dinocysts along time. Changes detected in the dinocyst community appeared to be coherent at sub-orbital and orbital scales with those detected with other sea-surface proxies and continental bio-indicators (pollen), demonstrating a close connection between sea-surface environments and the Iberian continent over the last 800 ka.

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9. Supplementary data

Supplementary data associated with this article can be found in the online version, at …

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Table caption

Table 1: key information regarding the set of cores used for this study.

Core	*Latitude*	*Longitude*	*Water depth (m)*	*Marine isotopic stage*	*References, Datasources*
IODP339 1385 D10H	**37.8**	**-10.02**	**3146**	**11, 19**	**This work,** Oliviera, Sanchez-Goni, in prep.
SU81-18	37.77	-10.18	3155	1	Le Coeur, L., unpublished; Turon et al., 2003
ODP976	36.20	-4.30	1108	1, 5, 11, 19	Combourieu Nebout et al., 1999; 2002; Levi C., unpublished; Rattinacannou J.-E., unpublished
MD95-2042	37.80	-10.17	3146	3, 5	Eynaud, 1999 ; Eynaud et al., 2000
MD95-2043	36.14	-2.62	1841	1,3	Rouis-Zargouni, 2010, Penaud, 2009
MD99-2339	35.89	-7.53	1177	1	Penaud, 2009, Penaud et al., 2011
MD04-2805CQ	34.52	-7.02	859	1	Penaud et al., 2010

Table 1

Figure / plate caption

Figure 1: (a) location of the cores of interest (IODP 339 U1385, SU81-18, MD95-2042, MD99-2339, MD04-2805CQ) with a sketch of the modern sea-surface hydrological dynamics (main currents, PC = Portugal current, CC = Canary current, NAD = North Atlantic drift); (b) detailed view of the modern surface dynamic structures, with: IPC: Iberian Poleward Current, AC: Azores Current, WIWF: Western Iberia Winter Front, after Peliz et al. (2005); and WAG: Western Alboran Gyre, EAG: Eastern Alboran Gyre, AOF: Almería-Oran Front after Hauschildt et al. (1999).

Green empty circle: "SHACK area" identifying the location of twin and/or proximal cores (i.e. SU81-18/ MD95-2042) of the "Shackleton site" - IODP 339 U1385.

Figure 2: Main dinocyst taxa shifts (relative abundances) over the "SHACK area" for the last one million years as depicted by a composite sequence consisting of interglacials from cores SU81-18 (e.g. Turon et al. 2003), MD95-2042 (e.g. Eynaud 1999; Eynaud et al. 2000) and IODP 339 U1385 (this work). Full interglacial conditions are highlighted by pink bands for LR04 Benthic $\delta^{18}O$ stack (Lisiecki and Raymo, 2005) values under 4 ‰.

Figure 3: (a) Comparison of interglacial signals along time and space of some selected dinocyst groups and species plotted versus isotopic $\delta^{18}O$ data of the respective cores, the LR04 Benthic $\delta^{18}O$ stack (Lisiecki and Raymo, 2005) and the 65°N summer insolation data (Berger and Loutre, 1991; pink band locate insolation values ≥ 450 $W.m^{-2}$). Mid-Brunhes Event (MBE) after Candy et al., 2010.

% *L.mac*. = relative abundances, i.e. percentages of *Lingulodinium machaerophorum;* Σ heterotr. dino. = sum of the relative abundances of heterotrophic dinocysts (taxa list after Marret and Zonneveld, 2003); Σ W. *Impagidinium* = sum of the relative abundances of the

warm *Impagidinium : I. patulum*, *I. paradoxum*, *I. aculeatum* and *I. sphaericum*). Yelow bands locate the Σ W. *Impagidinium* maxima on the "SHACK area".

(b) synchronisation of the Σ W. *Impagidinium* signals from cores SU81-18 (e.g. Turon et al. 2003) , MD95-2042 (e.g. Eynaud 1999; Sànchez-Goñi et al., 1999; Eynaud et al. 2000; Sànchez-Goñi et al., 2008) and IODP 339 U1385 (this work) over Terminations 1, 2 and 9 in concordance with the LR04 Benthic δ^{18}O stack (Lisiecki and Raymo, 2005). Note the good coherency of dinocyst derived data (suborbital events included) along comparable sections.

Figure 4: Sea-surface key proxies (from dinocysts, foraminifera and alkenones) compared to continental ones (Mediterranean forest) over a composite sequence gathering data from cores SU81-18 (e.g. Le Coeur, 1993, Turon et al., 2003), MD95-2042 (e.g. Sanchez-Goñi et al., 1999; Eynaud et al., 2000; Sanchez-Goñi et al., 2008) and IODP 339 1385 (this work, Sanchez-Goni et al., in progress, Oliviera et al., in progress). Derived SST from alkenone data: for MIS 1 and 5 from core MD95-2042 after Pailler and Bard (2002), for core MD01-2443 after Martrat et al. (2007). Percentages of the polar taxa *Neogloboquadrina pachyderma* sinistral (Nps) after Turon et al; (2003) for core SU81-18, after Sanchez-Goni et al., (2006) for core MD95-2042 and after Voelker and de Abreu (2011) for core MD01-2443. Marine isotopic stage limits after Lisiecki & Raymo (2005). Note the progressive regression of the *S. ramosus* through time.

Figure 5: Compilation of some archives of interest along the last 810 ka with: (a) Eccentricity cycles (after Berger & Loutre, 1991),(b) LR04 Benthic δ^{18}O stack (Lisiecki and Raymo, 2005), (c) CO_2 data (ppmv) compiled from Antarctic Ice Cores (from http://ncdc.noaa.gov/paleo/study/17975), (d) IODP339 U1385 XRF data Log (Ca/Ti) after Hoddel et al. (2013), (e) Dust content in the marine core MD03-2705 (terrigeneous content 100% - CaCO3) after Malaizé et al. (2012), (f) Mean Grain Size (normalized) after Clemens et al. (2008), (g) periods of strong Aguhlas linkage (adapted from Caley et al., 2012). These sequences are compared to (h) the dinocyst W/(W+C) ratio from the Alboran ODP976 site and from the "SHACK" area (SU81-18 / MD95-2042 and IODP 339 U1385), together with the

PCA analysis results of this composite dinocyst record (see methods) as seen throughout the first 3 components (from F1 (i) to F3 (k), representing 30% of the total variance).

Plate 1: Some common specimens from IODP 339 1385 (HoleD). Scale bar = 50 µm. (a) *Impagidinium patulum*; (b, h) *Selenopemphix nephroides*; (c) *Spiniferites membranaceus*; (d) *Stelladinium stellatum*; (e) *Spiniferites lazus*; (f) *Brigantedinium carioense*; (g) *Impagidinium aculeatum.*

Figure 1

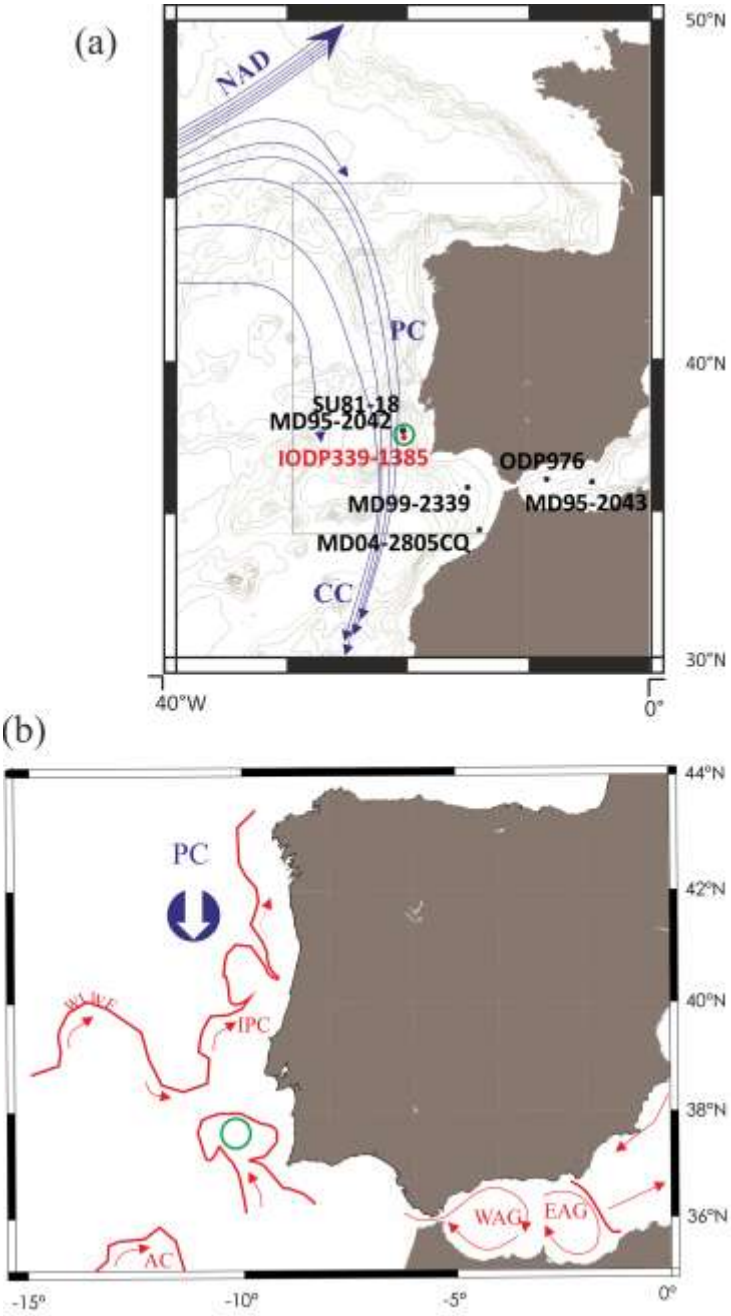


Figure 2

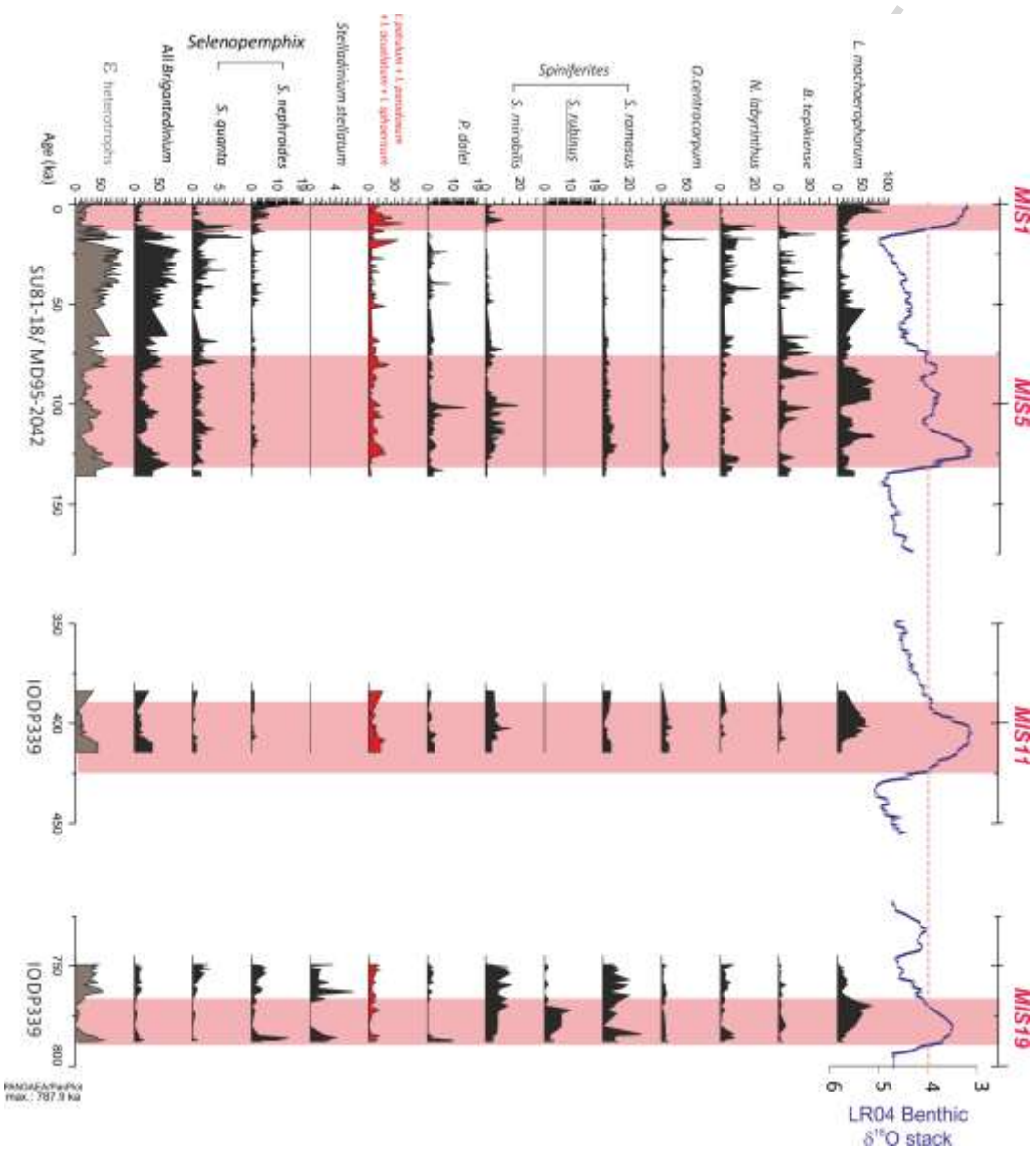


Figure 3

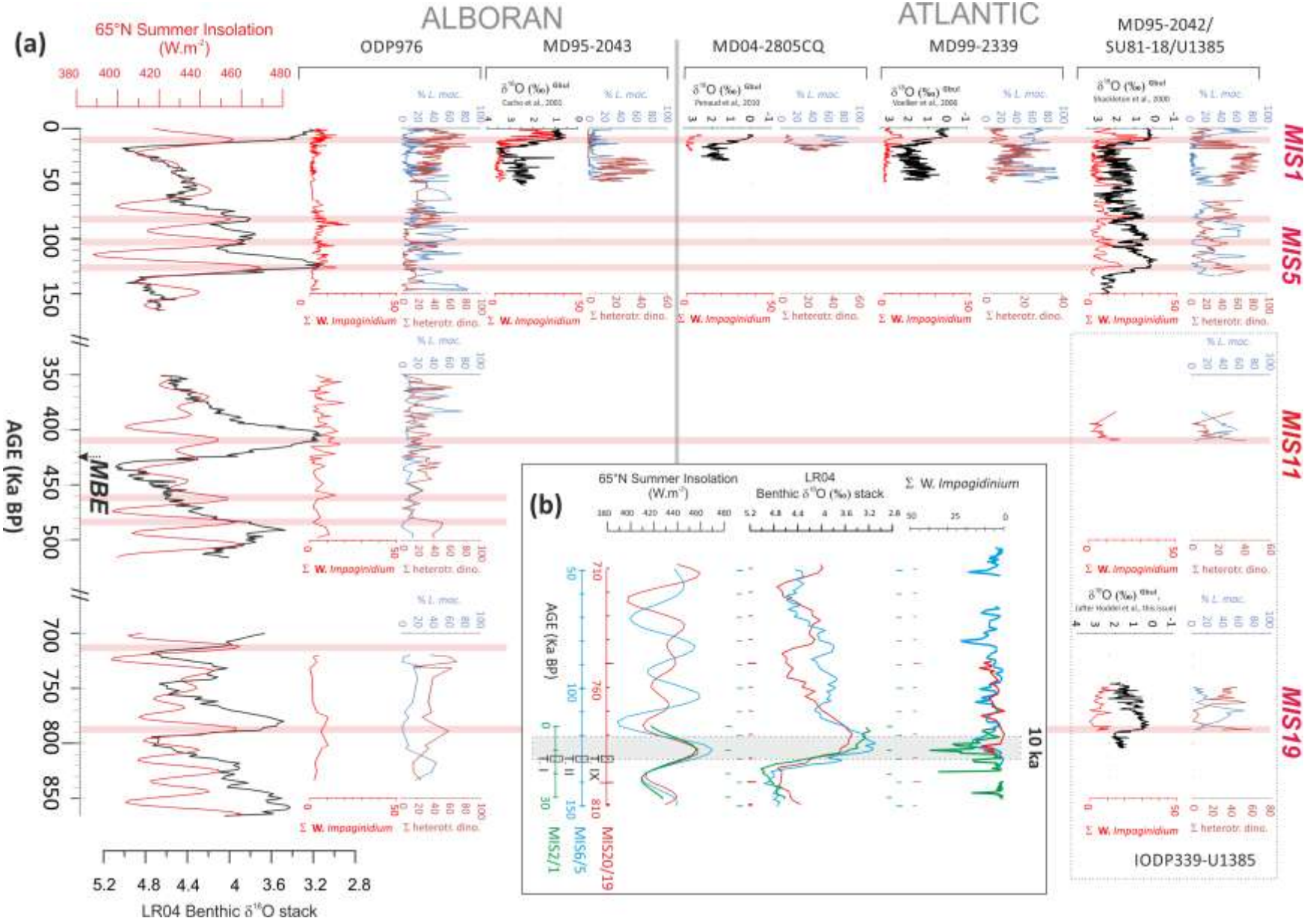

(a)
65°N Summer Insolation (W.m-2)
ALBORAN
ATLANTIC
ODP976
MD95-2043
MD04-2805CQ
MD99-2339
MD95-2042/ SU81-18/U1385
MIS1
MIS5
MIS11
MIS19
MBE
AGE (Ka BP)
LR04 Benthic δ18O stack
(b)
LR04 Benthic δ18O (‰) stack
Σ W. Impagidinium
10 ka
IODP339-U1385

Figure 4

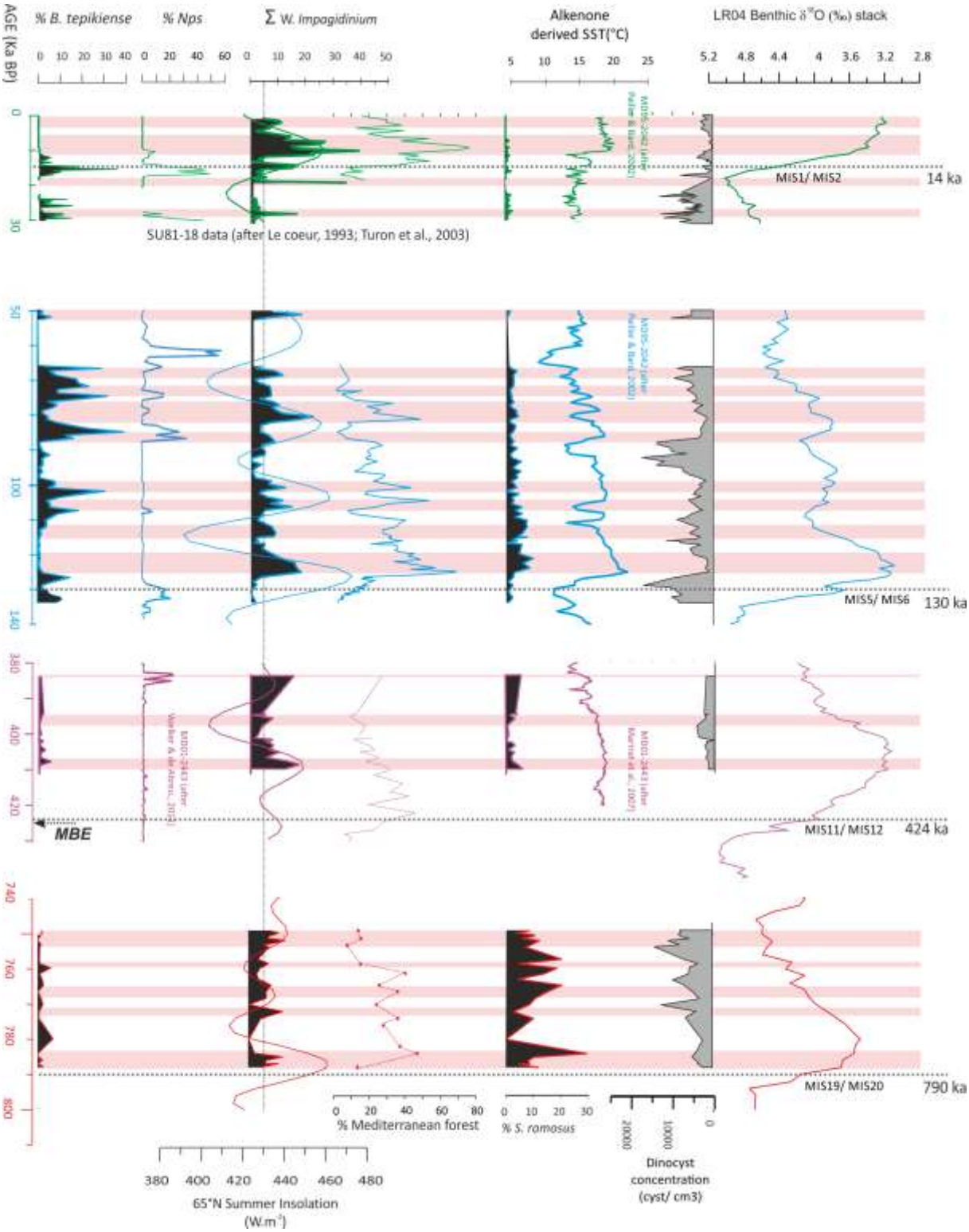
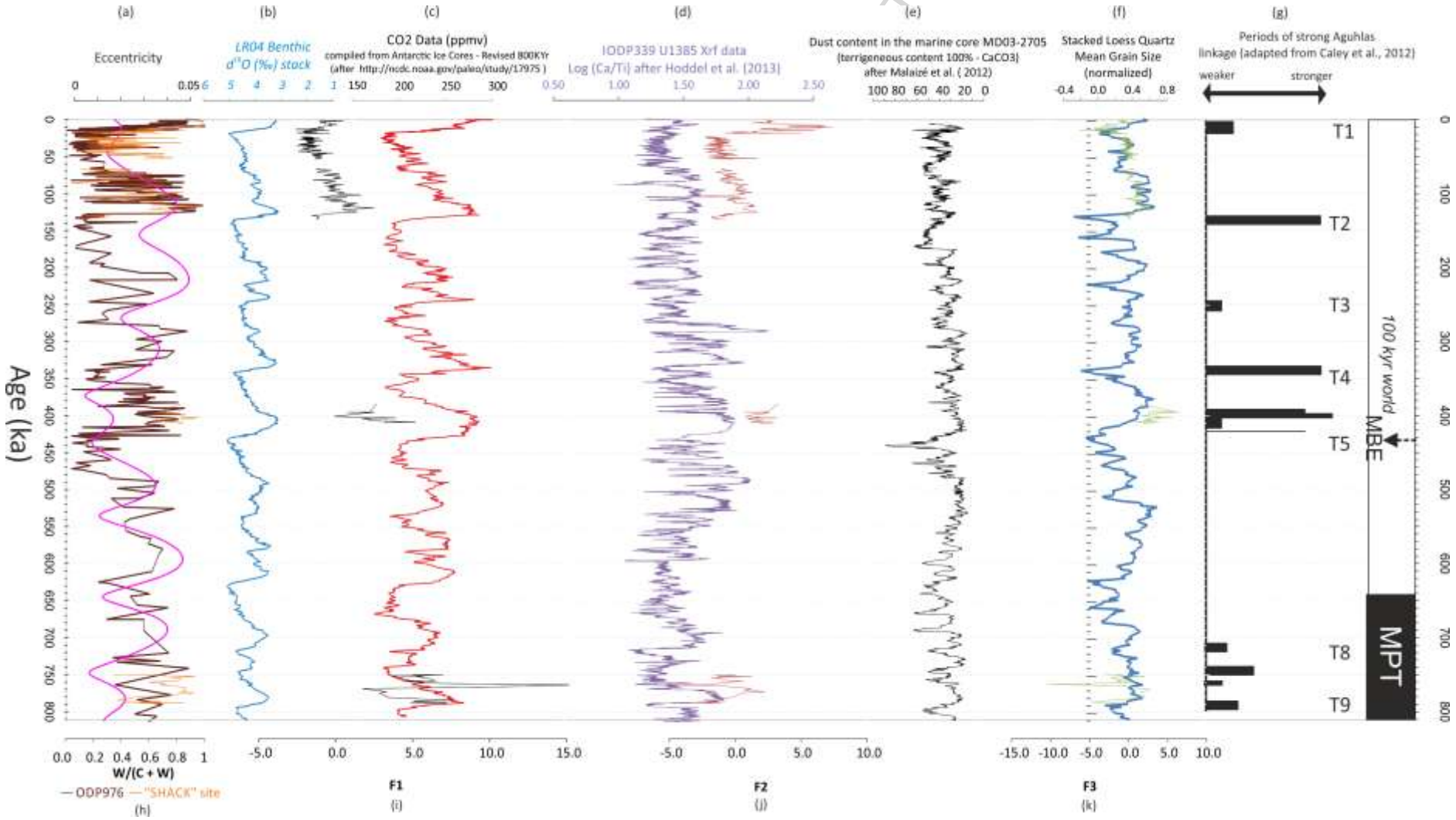


Figure 5



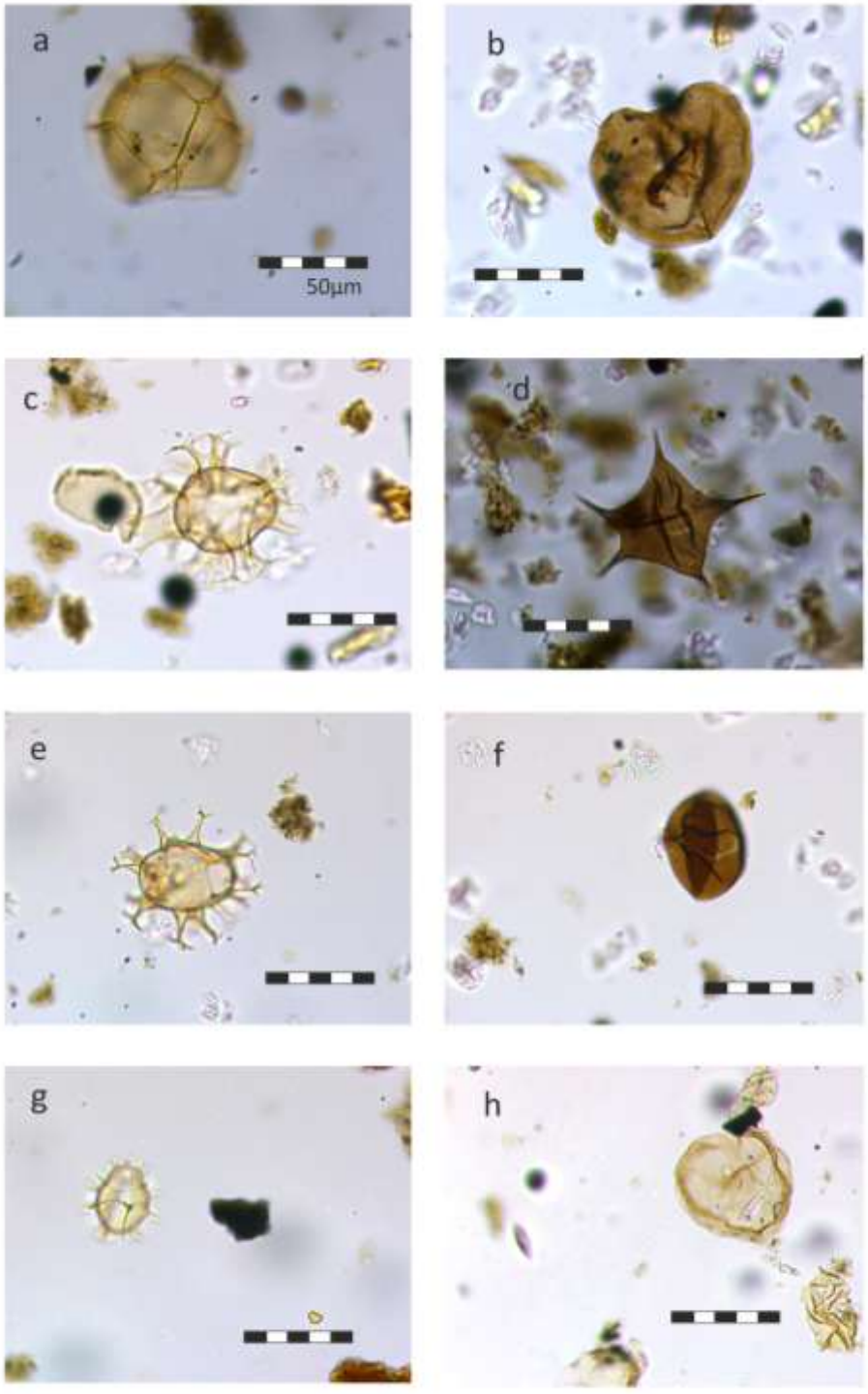
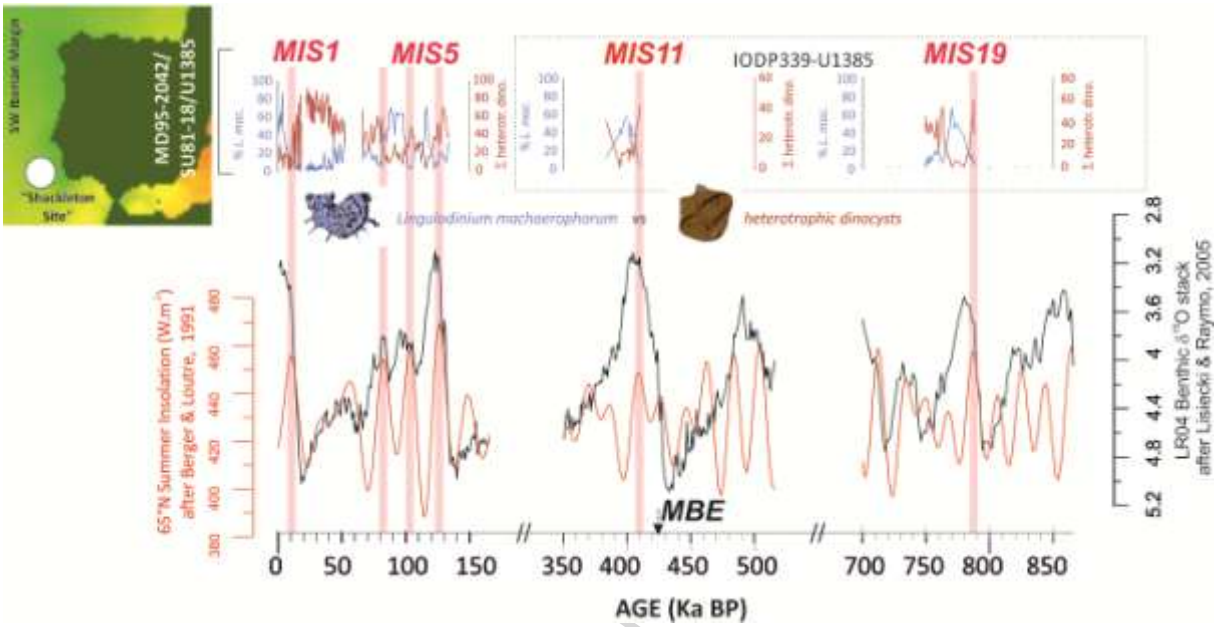


Plate 1



Graphical abstract

Highlights

Southern Iberian margin dinocysts are studied from long sedimentary records (including IODP site U1385)

Evolution of dinocyst populations is analyzed over the last 800 ka focusing on past interglacials

Coherent and reproducible patterns are detected within dominant cyst species on long term trends

Mediterranean /Atlantic exchanges are illustrated based on the comparison of inter-basin populations